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Kristen E. Crandell[1], Anthony Herrel[2,3], Mahmood Sasa[4,5], Jonathan B. Losos[6], Kellar Autumn[7]

1.Field Research Station at Fort Missoula, Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA

email : kristen.crandell@umontana.edu

2. UMR 7179 C.N.R.S/M.N.H.N., Département d'Ecologie et de Gestion de la Biodiversité, 57 rue Cuvier, Case postale 55, 75231, Paris Cedex 5, France.

3. Ghent University, Evolutionary Morphology of Vertebrates, K.L. Ledeganckstraat 35, B-9000 Gent, Belgium

4. Palo Verde Biological Station, Organization for Tropical Studies, 0676-2050 San Jose, Costa Rica

5. Instituto Clodomiro Picado, Universidad de Costa Rica, San Jose, Costa Rica

6. Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA

7. Department of Biology, Lewis & Clark College, Portland, OR 97219, USA

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ABSTRACT

Exploring the relationship between phenotype and performance in an ecological and evolutionary context is crucial to understand the adaptive nature of phenotypic traits. Despite their ubiquity in vertebrates, few studies have examined the functional and ecological significance of claw morphologies. Here we examine the adhesive toepad and claw system of *Anolis* lizards. Claw characters are significantly different between lizards classified as arboreal (perch height > 1 m) and non-arboreal (perch height < 1 m). Arboreal species possess significantly higher and longer claws, and show trends toward decreased claw curvature and wider claw tip angles. Toepad size and claw length and height are tightly correlated with each other and with perch height, suggesting that the adhesive toepad and gripping claw have co-evolved to accommodate different habitats. The functional morphology and evolution of claws are ripe areas for future investigation.

INTRODUCTION

Studying the link between phenotype and performance is necessary for insight in to the adaptation of form and function (Arnold, 1983). The functional significance of claws is not well studied, despite their ubiquity throughout vertebrates. Claws are known to increase available habitat (Cartmill, 1974), yet the link between morphological and habitat use variation is unknown. Here, we explore the claw in relation to a second structure used in attachment, the adhesive toepad, in *Anolis* lizards.

Anoles are an ideal model organism with which to unravel potential ecological contributions of claws, as they occupy a vast array of habitats with predictable evolutionary trajectories (Losos, 2009). *Anolis* lizards comprise a diverse clade that has undergone adaptive radiation on the Caribbean islands of the Greater Antilles, producing species of similar ecology and morphology termed "ecomorphs" that have evolved independently on each island (Williams, 1983). These lizards have been the focus of many studies examining the relationships

between morphology, performance, and ecology (see Losos, 2009 for a review). A particularly striking feature of anoles is the adhesive toepad, which enables the animal to move across smooth substrates with little difficulty. Toepads are thought to be a key innovation in anoles because their evolution may have allowed these lizards to occupy a larger portion of the available habitat than previously possible, thus permitting their radiation and diversification (Warheit et al., 1999).

Toepads are effective in permitting anoles to expand their habitat use due to their attachment abilities: they function best on smooth surfaces, such as leaves and smooth tree bark. Microscopic hair-like structures on the ventral pad, termed setae, adhere to substrates via van der Waals forces (Autumn et al., 2002; Puthoff et al., 2010). Among anole species, clinging ability varies with habitat use. Species that occur higher in the tree canopy possess larger toepads, and are capable of producing greater shear forces (Elstrott and Irschick, 2004; Macrini et al., 2003). This variation suggests that the evolution of adhesive toepads may have been critical for occupation of arboreal habitats, and thus may have played a major role in the diversification of Caribbean anoles into a distinct set of ecomorphs.

An often-neglected feature of *Anolis* relevant to clinging is their claws. Like almost all other lizard species, anoles possess claws, and variation in claw morphology may be related to differences in habitat use. Unfortunately, claws have been overlooked not only in anoles, but also in most amniotes. Vertebrates with claws can occupy larger portions of the habitat than non-clawed animals (Cartmill, 1974). However, the functionality of claws is less understood (see Maddin and Reisz, 2007 and Zani, 2000). Some aspects of claw shape are known to affect attachment ability, including claw height (the distance measured from dorsal to ventral at the base of the claw Zani, 2000). In animals such as beetles, claws interact with surface irregularities in two ways: interlocking and friction. When surface irregularities are larger than claw tip diameter, the claw mechanically interlocks with the irregularities. In contrast, when surface irregularities are smaller than claw tip diameter, attachment results from frictional forces. In this instance, if the tangent

between the claw and the irregularity is too low, the claw slips (Dai et al., 2002). As such, mechanical interlocking (accomplished with a smaller claw tip relative to substrate roughness) is often times stronger than frictional attachment, with a lower likelihood of failure. Thus, the ability to create a mechanical attachment, rather than a friction-based attachment, is improved with smaller claw tips. Decreasing the size (or effective angle) of the tip increases the likelihood of surface irregularities being larger, offering more opportunity for mechanical attachment. In fact, in artificial claws, decreasing the tip's effective angle significantly improves the strength of attachment (Provancher et al., 2004).

However, understanding the broader relationship between claw morphology and habitat use is not yet possible. A study linking claw morphology directly to habitat use in birds indicates that ground-dwelling species have significantly less curved claws than perching species, and species that climb have claws with higher curvature than both ground and perch dwellers (Feduccia, 1993). Similar patterns have been observed in lizards: arboreal and saxicolous species have claws with higher curvature (Tulli et al., 2009). Some additional evidence for the importance of claws exists in a single species, the ecologically variable *Anolis cybotes*; individuals in more rocky areas appear to have more curved claws (Wollenberg et al., 2013).

It is reasonable to predict that the claw and adhesive toepad operate under disparate conditions. The toepad functions best on relatively smooth, homogenous surfaces. The attachment between microscopic hair-like structures of the ventral pad and the surface is modeled to be maximal on smoother surfaces (Persson and Gorb, 2003; Russell and Johnson, 2013), and performance declines with increasing surface roughness (Vanhooydonck et al., 2005). In contrast, claws appear to maximize functionality on very rough surfaces, where mechanical interlocking of the claw is often-times stronger than friction forces on smoother surfaces (Dai et al., 2002). Thus, it appears both structures are optimal in two different scenarios. This observation was first put forth by Mahendra (1941), who observed following claw removal, *Hemidactylus* geckos were unable to attach to rough surfaces, but

attachment to smooth surfaces was unaffected. Further recent explorations are limited, but best evidenced in an analysis of performance and morphology. Zani (2000) found that in 85 species of lizard, toe width and lamellae number is correlated with attachment ability to smooth surfaces, while claw height is correlated with rough surface attachment.

Examining both the adhesive toepad alongside the claw may reveal ecological patterns hitherto unknown, or previously overlooked and attributed to toepad function alone. Here, we explore the relationship between toepad clinging ability, claw morphology, and habitat use in *Anolis*. We test for associations between claw morphology and habitat use. We predict that arboreal species with higher perch heights will have claw morphologies associated with improved attachment abilities: higher and longer (Zani, 2000), more curved (Feduccia, 1993), and sharper tips (Dai et al., 2002). We also test if phylogenetically corrected features of claws that are thought to improve attachment co-vary with toepad adhesion ability, given that toepads also correlate with habitat (Elstrott and Irschick, 2004). Our available lizards are mainland species, and as such we also confirm that mainland species follow the same trends as island species by testing for a positive relationship between toe force production and perch height (Irschick et al., 1997; Macrini et al., 2003).

METHODS

Study area and species

Fieldwork occurred at La Selva Biological Station, Playa Piro, and Palo Verde Biological Station in Costa Rica, and Gamboa, Panama. A total of 12 species was studied (see table 1). To capture animals and determine perch height, we walked along trails daily when lizards were active and recorded data for any individual sighted. Perch height was measured as distance from the ground to the individual's

original position, and perch diameter was measured at the location the lizard was first observed. Lizards were captured by hand or noose and kept for no longer than 48 hours. Lizards were kept in one-gallon plastic bags, transported to the field lab and returned to their original location following performance trials.

Adhesion performance

Following capture, one person (KEC) took shear-force measurements. A dual-range force sensor (Vernier) was attached to a vertical acetate covered glass microscope slide with a custom plexiglass attachment and butterfly clip. For each subject, the fourth (longest) digit was isolated and gently applied to the acetate sheet (Fig. 1). These performance measures only reflect attachment ability of the adhesive toepad, not the claw, because the claw was not able to penetrate the acetate coating. The anole was pulled by hand at an approximately constant speed, and the shear force was recorded at 40 Hz. Each subject underwent three repeated trials for left and right fourth toe.

Morphology

For all species in this study, we measured toepad and claw morphological characters from preserved specimens at the Museum of Comparative Zoology, Harvard University, and specimens from the Museum of Southwestern Biology, University of New Mexico (see appendix for list). A scanner (Epson Perfection 4900 and V500) digitized images of the fourth right hind digit, with the claw flattened sagitally against the scanner. Measurements were taken with ImageJ (1.4g, Rasband). Morphological characters of the toe included toepad area, measured from where the pad begins to widen (i.e., where the next most distal lamellae is longer than the previous), and lamellae number, counted as lamellae contained within toepad area. Measurements of the claw included: height, length, curvature (as measured by Zani, 2000), and tip angle (Fig. 2).

Analysis

For all species, we determined descriptive statistics for all continuous characters. To meet assumptions of normality and homoscedasticity, all measurements except for toepad force and claw tip angle were log-10 transformed prior to analysis. We corrected for size in characters that significantly correlated with SVL. To do so, we regressed log-10 adjusted values against log-10 adjusted SVL and calculated residuals, which were used for subsequent regressions.

A bivariate Pearson correlation on the log-10 transformed data was used to determine correlations among traits. Log-10 transformed data were then used as input for an independent contrasts analysis (Felsenstein, 1985) using the GEIGER package in R (Harmon et al., 2008). The most complete phylogenetic tree of *Anolis* (Nicholson et al., 2005) served as the basis for analyses (Fig. 3). Panamanian species described in Castañeda and de Queiroz (2013) were added as sister taxa, and *Anolis apletophallus* was placed as sister taxon to *Anolis limifrons* (S. Poe, pers. comm.). Branch lengths of the phylogeny were unknown, and were set to arbitrary lengths using a Grafen transformation (Grafen, 1989). The calculated residual values of morphological, performance, and habitat use variables were input into a linear regression analysis to determine correlation coefficients. An analysis of variance (ANOVA) tested for statistical significance for all regressions. All analyses presented account for phylogeny.

We also compared claw variables between two groups of anoles classified as "arboreal" or "non-arboreal." Arboreal species were defined as those with an average perch height greater than one meter, whereas non-arboreal were those found perching below one meter. Species with mean perch heights less than one meter are generally seen on or near the ground, whereas those above one meter are those that are often seen in the canopy. Claw morphologies (claw curvature, claw tip angle, claw height, and claw length) were first compared with a phylogenetically corrected MANOVA. Each character was then compared between groups with a phylogenetically corrected ANOVA. One-tailed tests were used in all comparisons, as

we had a-priori predictions for claw curvature (Feduccia, 1993), claw tip angle (Dai et al., 2002), and claw height and length (Zani, 2000). It should be noted that Zani (2000) found the correlation between claw length and clinging ability on rough surfaces was not robust to changes in phylogenetic branch lengths in one out of four models. Both phylogenetic analyses used the GEIGER package in R (Harmon et al., 2008).

RESULTS

Morphology and performance

Table 1 lists the mean $\pm$ SE for all morphological variables and toepad force production. All variables were size corrected, with analyses performed on the residuals of the data regressed against body size (see methods), with the exception of claw tip angle ($p=0.68$, $r^2=0.02$) and claw curvature ($p=0.91$, $r^2= 0.001$), because they were uncorrelated to overall body size. All correlations are the result of phylogenetically independent contrasts to account for ancestral relatedness.

Adjusted toepad area correlates positively with the size adjusted variables claw height ($p<0.001$, $r^2=0.65$, d.f.=1,10), claw length ($p=0.03$, $r^2=0.35$, d.f.=1,10), and non-size adjusted claw curvature ($p=0.05$, $r^2=0.26$, d.f.=1,10). Pad area also correlates positively with toepad force production following corrections for size ($p<0.001$, $r^2=0.75$, d.f.=1,10). Toepad lamella number exhibits similar relationships, correlating positively with claw height ($p=0.02$, $r^2=0.42$, d.f.=1,10), claw length ($p=0.03$, $r^2=0.38$, d.f.=1,10), and toepad force production ($p<0.001$, $r^2=0.83$, d.f.=1,10).

A positive correlation also occurs between toepad force production and claw height ($p=0.01$, $r^2=0.51$, d.f.=1,10) and claw length ($p=0.02$, $r^2=0.46$, d.f.=1,10) (Fig. 4). Force production and claw curvature are also related, but the relationship is not statistically significant ($p=0.08$, $r^2=0.30$, d.f.=1,9). No relationship is present between force production and claw tip angle ($p=0.98$, $r^2<0.0001$, d.f.=1,10).

Habitat use

A positive correlation exists between perch height and toepad shear-force ($p=0.006$, $r^2=0.58$, d.f.=1,9) (Fig. 5), but no correlation occurs between adjusted force production and perch diameter ($p=0.22$, $r^2=0.16$, d.f.=1,9). Perch height does not linearly correlate with claw variables, including claw height ($p=0.43$, $r^2=0.07$, d.f.=1,9), claw length ($p=0.26$, $r^2=0.14$, d.f.=1,9), claw curvature ($p=0.56$, $r^2=0.04$, d.f.=1,9), and claw tip angle ($p=0.90$, $r^2=0.002$, d.f.=1,9).

We also compared claw variables with binomially categorized habitat by dividing anoles in to two classes: "arboreal," with average perch heights of over one meter, and "non-arboreal," with average perch heights below one meter. We found general trends in all claw morphologies between our arboreal categories (phylogenetic MANOVA $p=0.054$). Claw tip angle was close to statistically different between categories ($p=0.054$, Fig. 6A), as was claw curvature ($p=0.054$, Fig. 6B). Both claw height ($p=0.007$, Fig. 6C) and claw length ($p=0.029$, Fig. 6D) were statistically significantly different between groups.

DISCUSSION

Our study is one of the first to examine toe and claw morphology in a vertebrate with an eye towards performance in a natural environment. We find support for both of our hypotheses. First, the adhesive toepad of *Anolis* species co-varies with claw morphology. Secondly, all claw characters measured are associated with habitat use.

We found strong evidence for co-evolution between adhesive toepads and claws in size-corrected correlations between toepad size and claw height and length (Fig. 4). Adhesive toepads and claws provide clinging capability in different substrate conditions: smooth and rough, respectively. Arboreal animals encounter both types of surfaces as they move on leaves, a smooth substrate, and woody

vegetation, a rough substrate; hence, it is not surprising that more arboreal species, needing greater attachment ability, should have better developed claws and toepads.

We found strong trends and significant differences between species grouped as arboreal (mean perch height > 1 m) and non-arboreal (mean perch height < 1 m). A phylogenetic MANOVA of all claw morphologies came very close to statistical significance at $p = 0.054$, indicating that claw characters are likely related to perch height. With phylogenetic ANOVAs for each character, we were able to dissect this trend. Claw curvature and claw tip angle were not statistically significant between groups, but both showed major trends in that direction, with p values very close to, but slightly above, 0.05. This trend does not fall in line with increased claw curvature in arboreal birds in comparison to ground-dwelling birds (Feduccia, 1993). Given that claw sharpness (measured here as a smaller tip angle) improves attachment ability (Dai et al., 2002; Provancher et al., 2004), it is also surprising that arboreal species trend toward less pointed claw tips. We predict with larger sample sizes, a significant trend would appear. These differences suggest further studies examining claw function are vital. Both claw height and length were significantly different between the two groups (Fig. 5). Claw height improves attachment ability on rough surfaces (Zani, 2000). Interestingly, adhesive pad area is also correlated with perch height (Elstrott and Irschick, 2004). Together, differences in claw shape and toepad function in comparison to perch height serve as further evidence for the co-evolution between claws and pads.

Despite strong differences between arboreal and non-arboreal morphologies, we did not find linear correlations between claw characters and perch height in this study. Arboreality implies a heightened need for both attachment systems, to maintain attachment during motion and to avoid falling. However, the functionality of these systems differs in their basic attachment mechanics. In particular, the toepad area is continuous with an increase in surface area of the pad resulting in an increase in clinging ability. In contrast, claw function may not be continuous – once a certain threshold is reached in size or shape, an increase in size or further changes

in shape may confer no more functional, and therefore selective, advantage. For example, higher claws may serve no better than slightly lower ones, as both are capable of mechanical interlocking with the substrate. This is in sharp contrast with toepad area, where increased size confers a linear increase in force. Thus, certain morphologies will be able to accommodate rough substrates, without regard to the actual perch height.

Our study focused on the two ecological standards for anoles: perch height and diameter. While we found several intriguing patterns with perch height, none of our measured variables correlated with perch diameter. In a study by Macrini et al. (2003), perch diameter in mainland and island anoles correlates with pad area. However, we found no such relationship here. Mainland species vary in habitat use, and with our relatively small sample size, such patterns may not appear due to higher ecological variation of mainland anoles (Schaad and Poe, 2010). Further, variation in claws may not reflect ecological differences on such a minor scale. In order to stay attached to a vertical perch, the forces produced by pushing the left and right limbs in to the perch must be 90 degrees or less in order to support body weight. Claws are known to help reduce this effective angle (Biewener, 2003; Cartmill, 1974). However, at perch diameters less than a body width, where most of our species were observed, claws are not necessary as the angle between limbs is much less than 90. Thus, a non-existent relationship between perch diameter and claw morphologies agrees with theory.

Claw characters may prove important in ecological contexts not reported in this study. In particular, claw height improves attachment ability on rough surfaces (Zani, 2000). Thus, we predict that improved claw morphology (height, length, curvature, and sharpness) is also correlated with surface roughness. This prediction is opposite that which is known in adhesive toepads, which function best on smooth surfaces (Vanhooydonck et al., 2005). Further, the functional interaction of claw and substrate is unknown. Claws may be used to actively pierce substrates, or attach solely due to passive friction. If claws are used to pierce, our results may be

confounded by the wearing-down of the claw structure, as observed in artificial claw systems (Provancher et al., 2004). Use of the claw is likely to vary with size and morphology of the vertebrate, as well as locomotor style. For example, birds show a variety of toe organizations – varying from one to two opposing toes in various configurations. Alongside the differences in muscular arrangement of the flexors and extensors, this variation may influence whether the claw is actively piercing or passively attaching to a substrate. Body size and shape has the potential to further confound claw use. For example, in four-legged vertebrates, the smaller species tend to have a more sprawled posture, while larger species are more upright (Biewener, 1989). The distance and angle between opposing limbs likely affects the effective angle of the claw relative to the substrate – especially on substrates with a limited diameter (Cartmill, 1974). Behavioral and ecological data in lizards would shed light on claw use, body size, and locomotion, yet are lacking for most of the species studied here. For studies outside of *Anolis*, understanding body size, posture, and foot morphology will be crucial to compare claw morphologies across taxa.

Lastly, although not the focus of our study, we found that mainland anoles studied here show similar ecological patterns to island species. In island species, toepad force production positively correlates with perch height (Elstrott and Irschick, 2004). This potential trend was unknown in mainland species, particularly because mainland species have dramatically smaller adhesive toepads (Macrini et al., 2003). Whether or not this difference in size indicates mainland species have less clinging ability remains to be tested, as island studies are not comparable to our data and appear more variable in sampling technique. Moreover, our study focused on a single digit, while previous studies measured force production in the 10 forelimb digits (Irschick et al., 1996). Additionally, mainland species might experience more diversity in textures and selection for claw characters might not be as strong as in an island setting. Understanding potential differences and similarities between clades is of particular interest, as island and mainland species appear to have different patterns of morphological variation (Schaad and Poe, 2010; Velasco and Herrel, 2007).

Further studies exploring both mainland and island species in tandem are necessary to elucidate how toepad morphologies differ between populations. Such studies must use caution when collecting or comparing adhesion performance data to previously published values. Our data were collected in the field and may have been influenced by environmental conditions including humidity, which may reduce (Niewiarowski et al., 2008; Stark et al., 2012) or increase (Chen and Gao, 2010; Pesika et al., 2009; Prowse et al., 2011; Puthoff et al., 2010) clinging ability in biological adhesives. In particular, high humidity environments change the mechanical properties of the microscopic setae, increasing adhesion abilities (Prowse et al., 2011; Puthoff et al., 2010). Similarly, increased stress of being sampled in the field may impair performance. Further studies across *Anolis* with standardized methods, alongside increased sample sizes, will improve our understanding of relationships among pad, claw, and habitat use.

Here we have shown the ecological importance of claw morphology. Anoles found higher in the forest have longer and higher claws, with trends toward decreased claw curvature and increased claw tip angle. These results indicate the importance of claws to habitat use. As almost all vertebrates have claws, this character is ripe for further study. Our study also indicates that claws and adhesive toepads have coevolved in *Anolis*. However, they likely serve partially differing functions; a hypothesis that requires further research on the interaction between the toe and natural surfaces. Understanding this interaction will entail an integration of micro-scale studies of single foot-hairs (Autumn, 2006; Autumn et al., 2000; Liang et al., 2000) and claw tips (Dai et al. 2002) with macro-scale studies of the interaction between a variety of natural and artificial surfaces with whole claws (Provancher et al. 2004) and toepads.

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Figures

Figure 1. *Anolis sagrei* hanging on a glass slide by a single toe.

Figure 2. Morphological characteristics determined for each digit. Claw height = length of line A; Claw Length = total length of segments C+D; Claw tip angle = Θ, Claw curvature = $57.296 * (2*\arcsin(((2*C^2*D^2) + (2*B^2*D^2) + (2*B^2*C^2) \pm B^4 \pm C^4 \pm D^4)^{0.5} / (2*C*D)))$ (modified from Zani, 2000)

Figure 3. Phylogenetic relationships of the 12 species in this study, modified from Nicholson et al. (2005). Branch lengths do not reflect distance.

Figure 4. Independent contrasts showing how toepad force production is correlated with claw height (A) and claw length (B), suggesting that both features have co-evolved in mainland *Anolis* lizards.

Figure 5. Independent contrasts showing that toepad force production is correlated with perch height in mainland *Anolis* lizards, illustrating that both traits have coevolved.

Figure 6. Claw morphological characters for species classified as arboreal (average perch height > 1 meter) and non-arboreal (average perch height < 1 meter). Claw curvature (a) and tip angle (b) are not statistically significantly different, but claw height (c) and length (d) are significantly different between groups.

Table 1. Morphological and performance characters measured for each species. All measurements were taken from the fourth (longest) digit of the right hind foot. Morphological measurements reflect museum specimens (supplement 1), and performance measures were taken from wild-caught individuals.

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Species	n (morphology)	n (performance)	SVL (mm)	Mass (g)	Claw height (mm)	Claw Length (mm)	Claw Curvature (degrees)	Claw Tip Angle (degrees)	Toepad Area (mm2)	Lamellae Number	Toepad Force (N)
Anolis auratus	11	6	42.66	1.35	0.32 ± 0.01	0.52 ± 0.03	40.13 ± 1.57	36.34 ± 2.99	1.06 ± 0.07	10 ± 0.23	0.0084 ± 0.00081
Anolis biporcatus	13	3	83.18	12.88	0.79 ± 0.02	1.10 ± 0.04	32.5 ± 0.39	34.39 ± 0.91	7.23 ± 0.34	18.7 ± .3	0.012 ± 0.022
Anolis capito	6	2	75.86	11.22	0.70 ± 0.05	0.90 ± 0.25	35.41 ± 0.91	29.06 ± 2.14	3.60 ± 0.39	12.3 ± 0.33	0.051 ± 0.021
Anolis cupreus	5	4	42.66	1.62	0.32 ± 0.02	0.35 ± 0.10	36.14 ± 1.33	31.60 ± 1.37	1.20 ± 0.23	9.0 ± 0.41	0.019 ± 0.0016
Anolis frenatus	7	9	93.33	17.38	1.14 ± 0.04	1.69 ± 0.1	33.07 ± 0.86	34.28 ± 0.98	18.60 ± 1.90	23.38 ± 1.07	0.15 ± 0.012
Anolis humilis	5	5	31.62	0.91	0.34 ± 0.05	0.52 ± 0.08	34.67 ± 1.03	28.57 ± 1.13	1.32 ± 0.26	10.8 ± 1.11	0.011 ± 0.0011
Anolis lemurinus	5	1	51.29	2.95	0.40 ± 0.01	0.50 ± 0.13	34.24 ± 0.80	35.52 ± 1.07	3.04 ± 0.27	14.0 ± 0.41	0.034 ± 0.0013
Anolis limifrons	7	5	38.02	0.95	0.31 ± 0.02	0.42 ± 0.03	34.07 ± 0.85	29.13 ± 1.64	1.53 ± 0.15	11.0 ± 0.49	0.0073 ± 0.0015
Anolis lionotus	10	7	64.57	5.50	0.46 ± 0.05	0.73 ± 0.11	35.47 ± 0.54	29.50 ± 1.35	3.44 ± 0.52	14 ± 0.24	0.020 ± 0.0013
Anolis pentaprion	9	2	48.98	2.45	0.43 ± 0.03	0.51 ± 0.03	32.91 ± 0.94	36.76 ± 1.27	2.83 ± 0.24	16.9 ± 0.28	0.092 ± 0.012
Anolis poecilopus	6	9	61.66	5.01	0.51 ± 0.05	0.83 ± 0.09	35.67 ±0.09	29.27 ± 0.66	4.20 ± 0.90	14.4 ± 0.68	0.032 ± 0.0014
Anolis polylepis	6	4	44.67	1.74	0.38 ± 0.02	0.34 ± 0.14	33.31 ± 1.59	31.89 ± 1.19	1.81 ± 0.11	11.8 ± 0.20	0.017 ± 0.0016

Table 1

Species	n (morphology)	n (performance)	SVL (mm)	Mass (g)	Claw height (mm)	Claw Length (mm)
Anolis auratus	11	6	42.66	1.35	0.32 ± 0.01	0.52 ± 0.03
Anolis biporcatus	13	3	83.18	12.88	0.79 ± 0.02	1.1 ± 0.04
Anolis capito	6	2	75.86	11.22	0.70 ± 0.05	0.90 ± 0.25
Anolis cupreus	5	4	42.66	1.62	0.32 ± 0.02	0.35 ± 0.10
Anolis frenatus	7	9	93.33	17.38	1.14 ± 0.04	1.69 ± 0.1
Anolis humilis	5	5	31.62	0.91	0.34 ± 0.05	0.52 ± 0.08
Anolis lemurinus	5	1	51.29	2.95	0.40 ± 0.01	0.50 ± 0.13
Anolis limifrons	7	5	38.02	0.95	0.31 ± 0.02	0.42 ± 0.03
Anolis lionotus	10	7	64.57	5.50	0.46 ± 0.05	0.73 ± 0.11
Anolis pentaprion	9	2	48.98	2.45	0.43 ± 0.03	0.51 ± 0.03
Anolis poecilopus	6	9	61.66	5.01	0.51 ± 0.05	0.83 ± 0.09
Anolis polylepis	6	4	44.67	1.74	0.38 ± 0.02	0.34 ± 0.14

Figure01

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Figure02

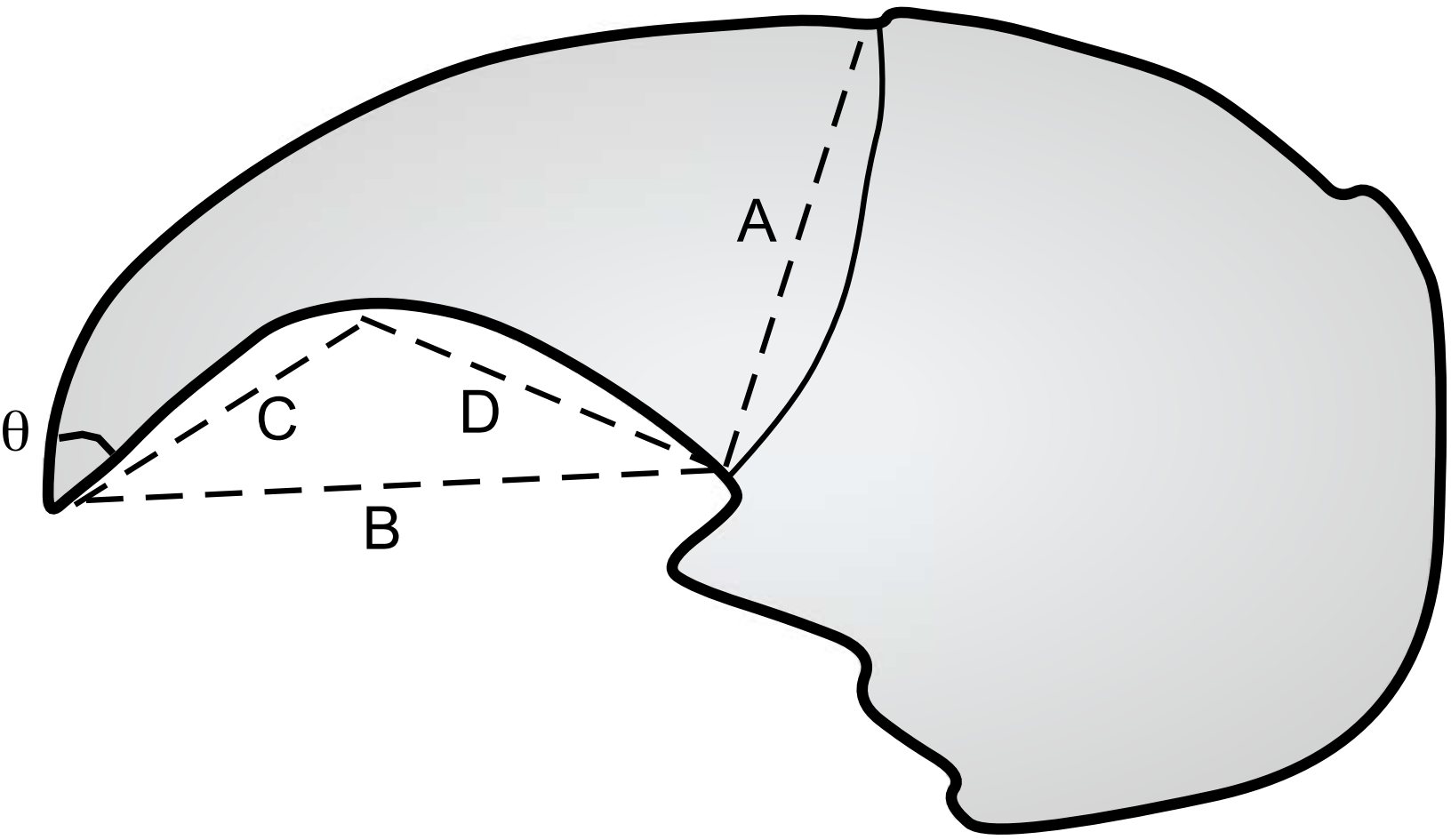


Figure03

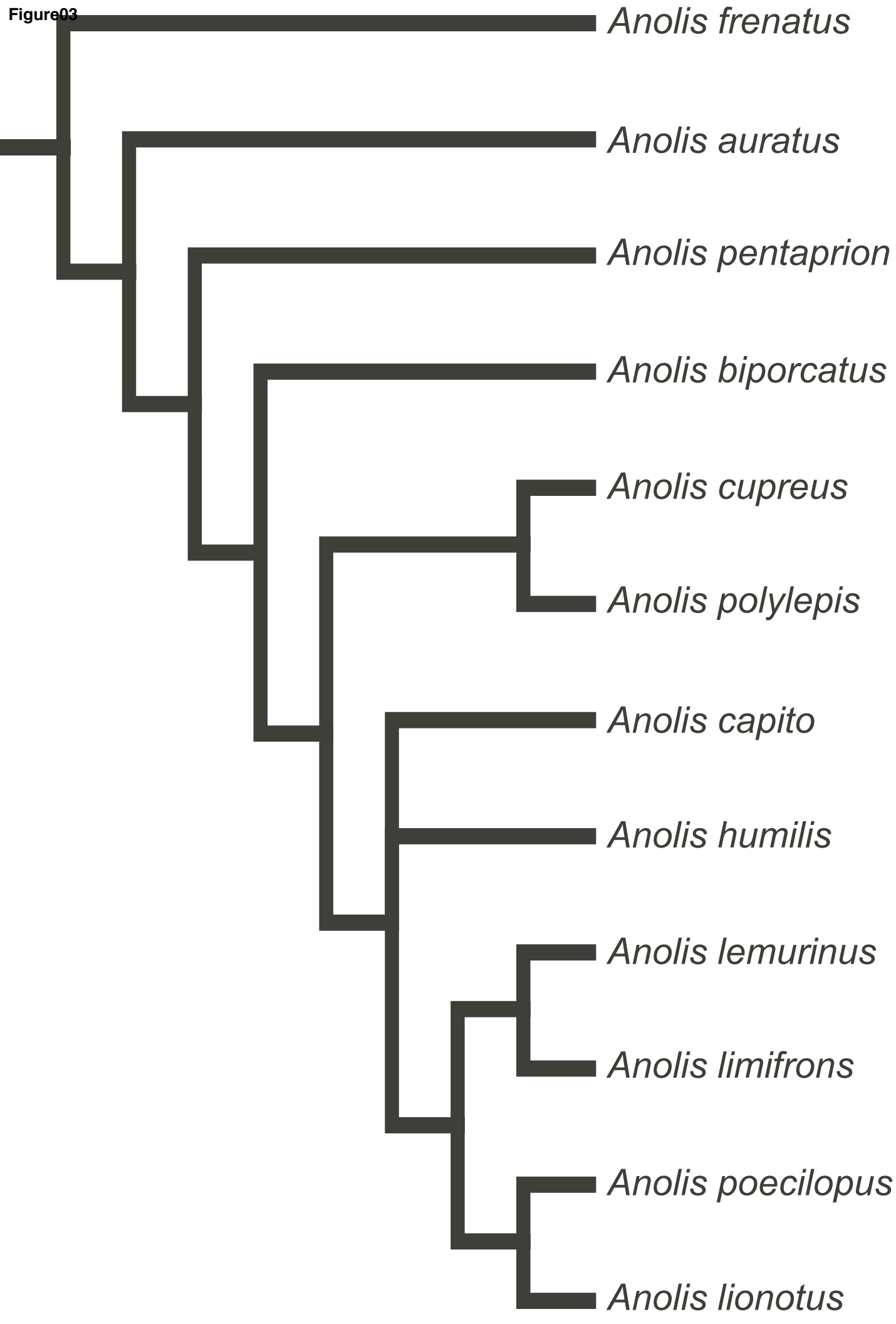
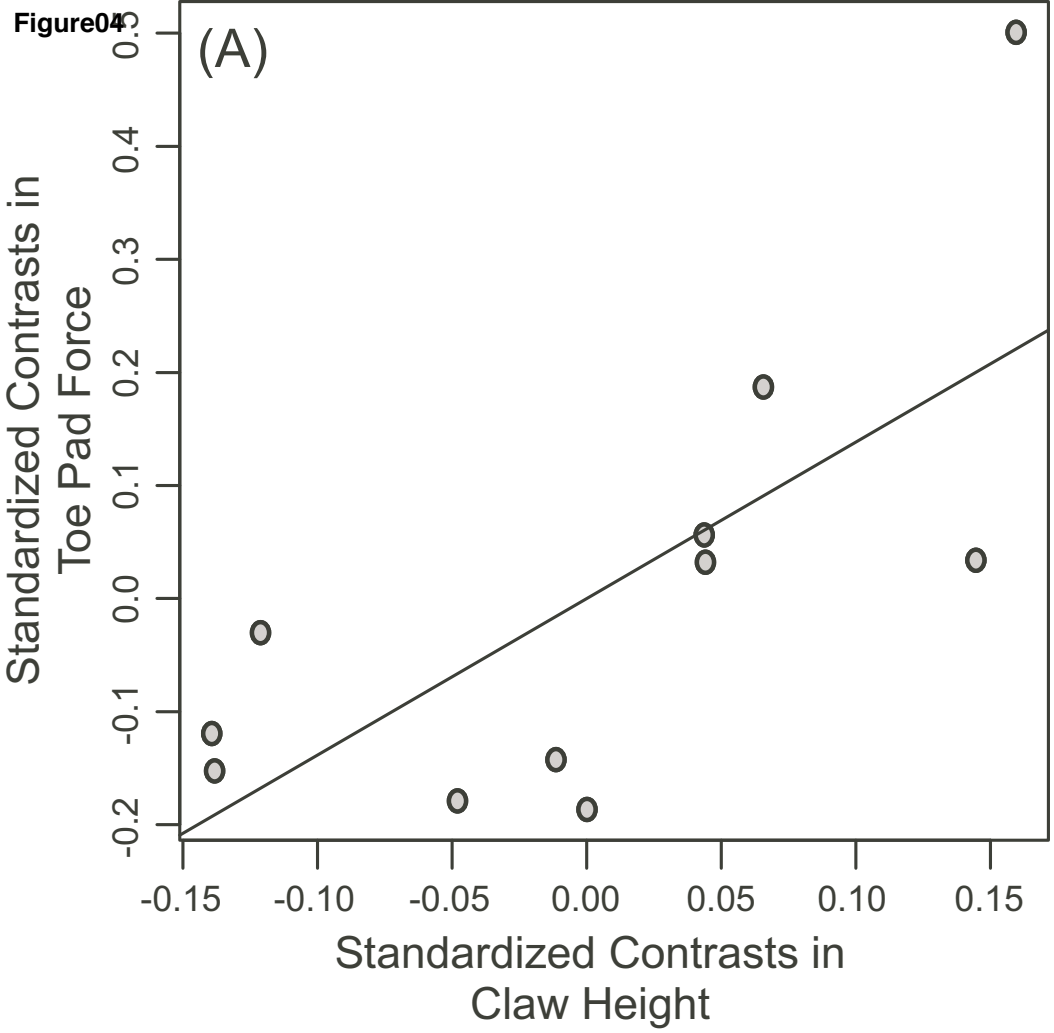

Anolis frenatus
Anolis auratus
Anolis pentaprion
Anolis biporcatus
Anolis cupreus
Anolis polylepis
Anolis capito
Anolis humilis
Anolis lemurinus
Anolis limifrons
Anolis poecilopus
Anolis lionotus

Figure04


(A)
Standardized Contrasts in Toe Pad Force
-0.2
-0.1
0.0
0.1
0.2
0.3
0.4
0.5
-0.15
-0.10
-0.05
0.00
0.05
0.10
0.15
Standardized Contrasts in Claw Height

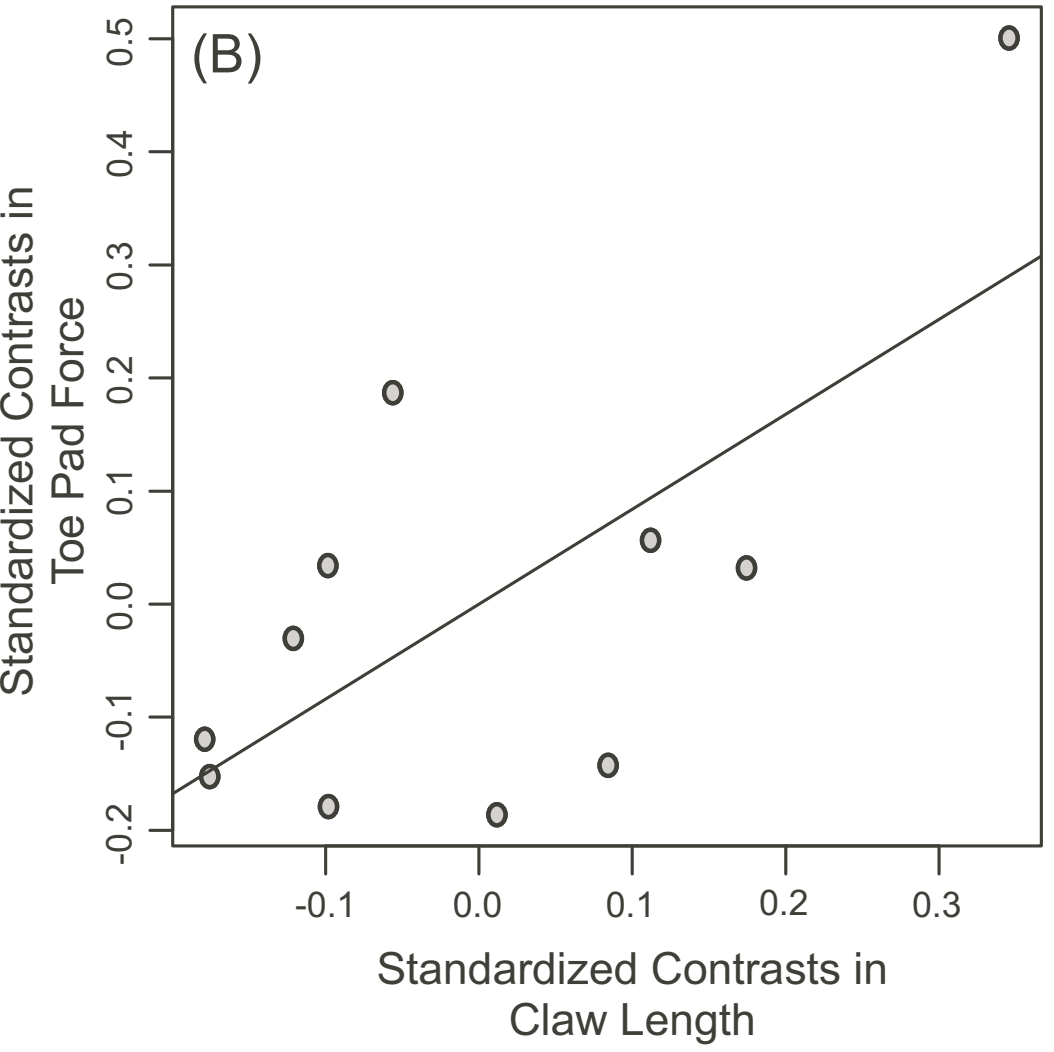

(B)
Standardized Contrasts in Toe Pad Force
-0.2
-0.1
0.0
0.1
0.2
0.3
0.4
0.5
-0.1
0.0
0.1
0.2
0.3
Standardized Contrasts in Claw Length

Figure05

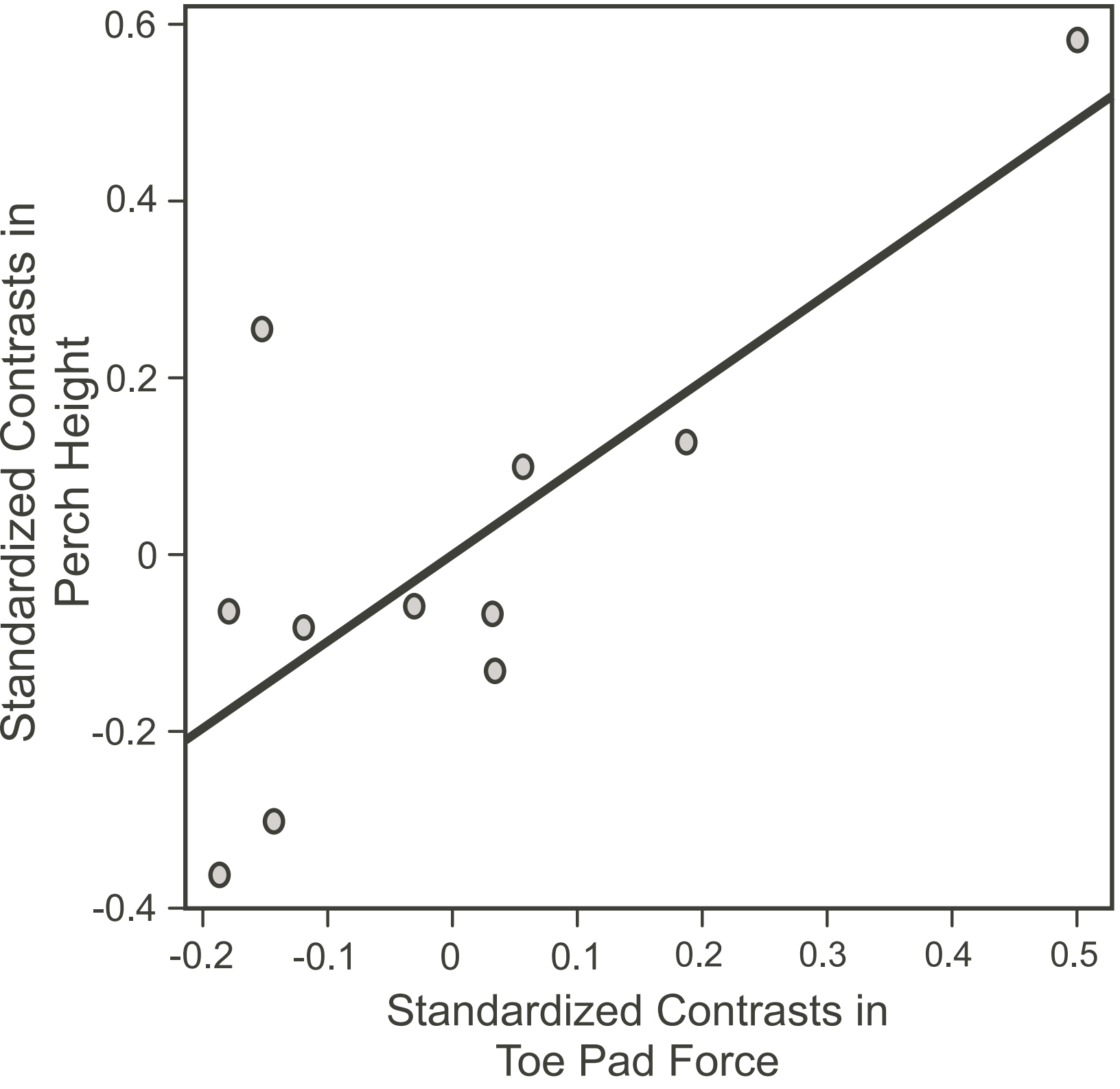
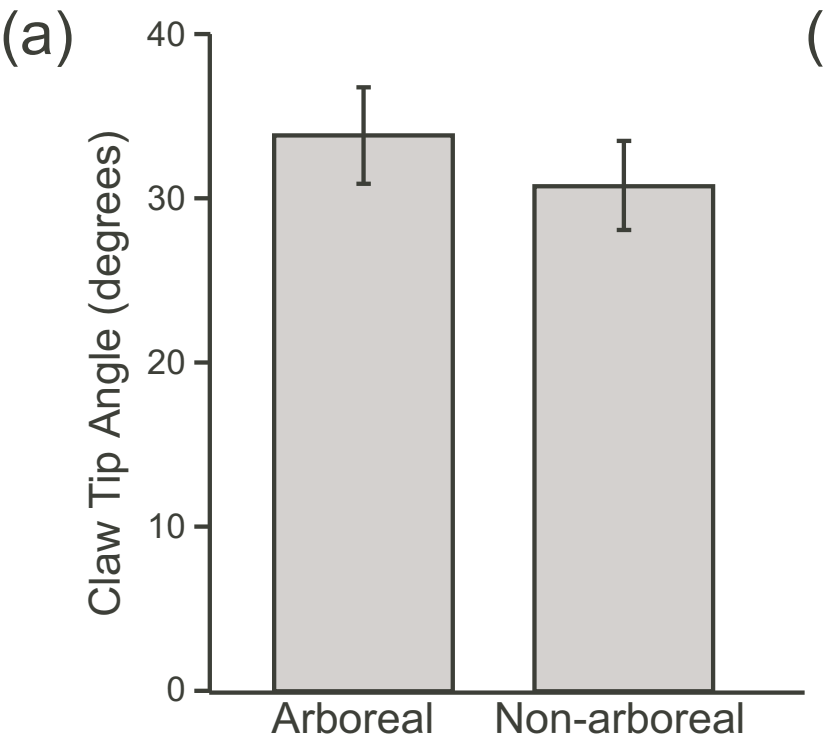
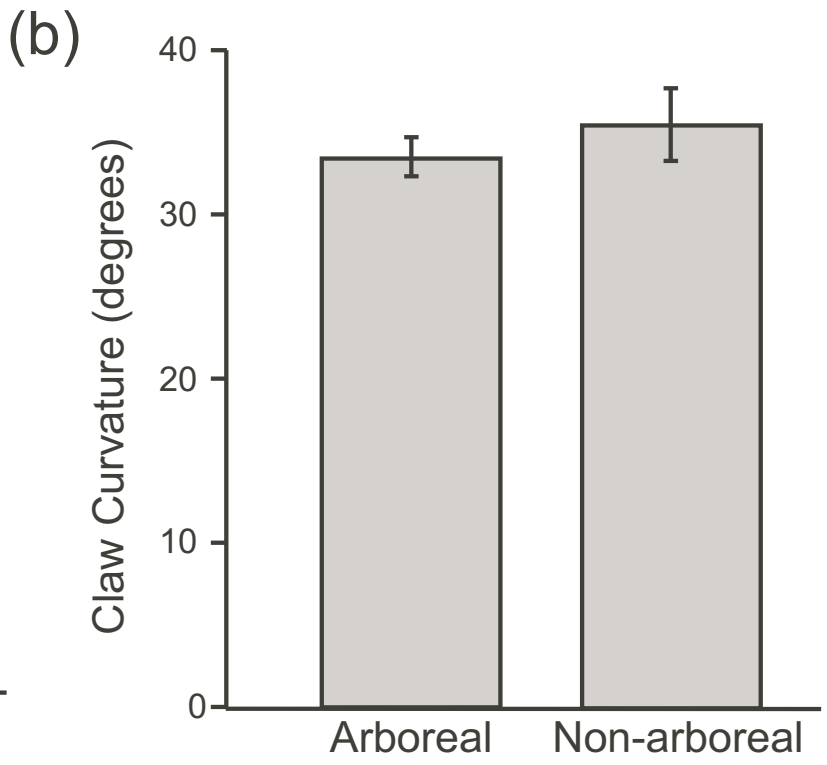
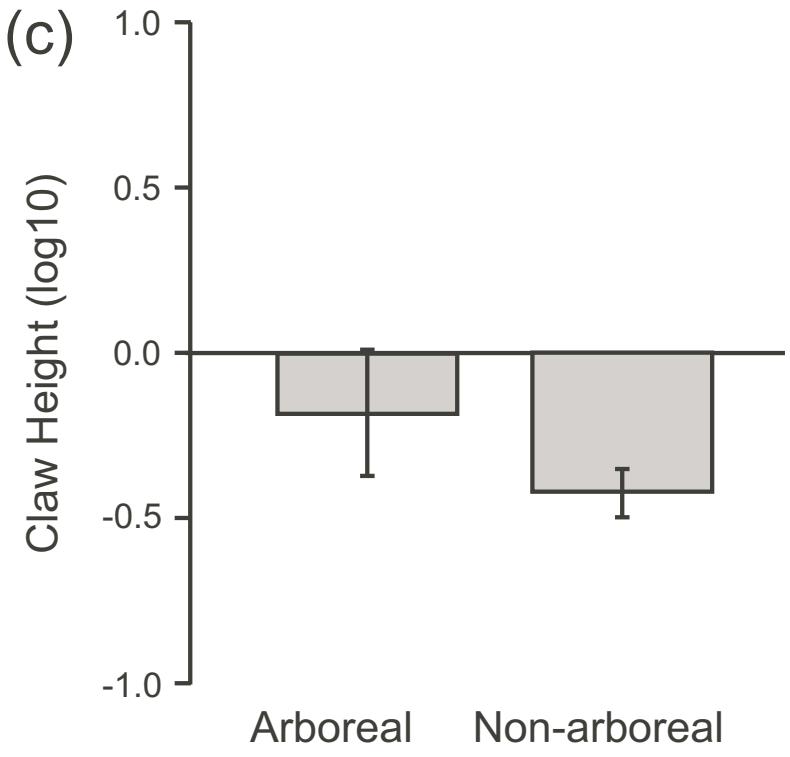
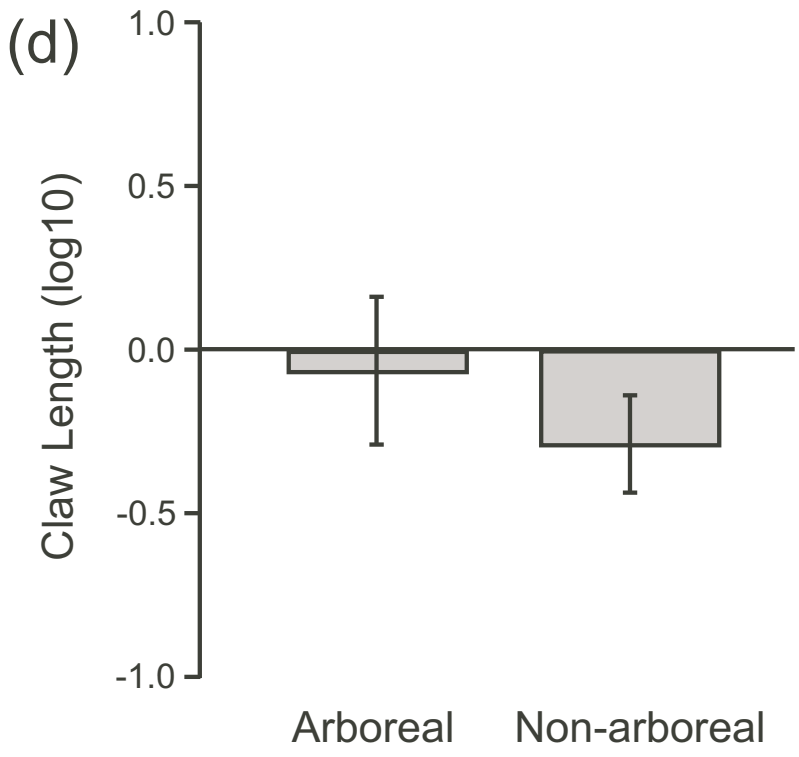

0.6
0.4
0.2
0
-0.2
-0.4
-0.2
-0.1
0
0.1
0.2
0.3
0.4
0.5
Standardized Contrasts in Perch Height
Standardized Contrasts in Toe Pad Force

Figure06


(a)
Claw Tip Angle (degrees)
40
30
20
10
0
Arboreal
Non-arboreal


(b)
Claw Curvature (degrees)
40
30
20
10
0
Arboreal
Non-arboreal


(c)
Claw Height (log10)
1.0
0.5
0.0
-0.5
-1.0
Arboreal
Non-arboreal


(d)
Claw Length (log10)
1.0
0.5
0.0
-0.5
-1.0
Arboreal
Non-arboreal

e-component

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